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Climatic water availability is the main driver of context-dependency of tree functional diversity effects on top and subsoil carbon storage in European forests

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Abstract (250 words)

The interplay of stand and environmental factors shape soil organic C (SOC) storage in forest ecosystems but little is known about their relative impacts in different soil layers. Moreover, how environmental factors modulate the impact of stand factors, particularly species mixing, on SOC storage, is largely unexplored. In this study conducted in 21 forest triplets (two-species mixed stand and respective monocultures nearby) distributed in Europe, we tested the hypothesis that stand factors (functional identity and diversity) have stronger effects on topsoil (FF+0-10 cm) C storage than environmental factors (climatic water availability, clay+silt content, oxalate-extractable Al - Al_{ox}) but that the opposite occurs in the subsoil (10-40 cm). We also tested the hypothesis that functional diversity improves SOC storage under high climatic water availability, clay+silt contents, Al_{ox}. We characterized functional identity as the proportion of broadleaved species (beech and/or oak), and functional diversity as the product of broadleaved and conifer (pine) proportions. The results show that functional identity was the main driver of topsoil C storage while climatic water availability had the largest control on subsoil C storage. Contrary to expectations, functional diversity decreased topsoil C storage under increasing climatic water availability but the opposite was observed in the subsoil. Functional diversity effects on topsoil C increased with increasing clay+silt content, while its effects on subsoil C was negative at increasing Al_{ox} content. This suggests that functional diversity effect on SOC storage along environmental gradients depends on the specific environmental factor and the soil depth under consideration.

Keywords: soil organic carbon; forest ecosystem services; triplets; oxalate-extractable metals; context-dependency effects; functional diversity

Three highlights (85 characters including spaces for each) – for a general reader

Impact of forest stand and environmental factors on soil C was investigated

Stand and environmental factors drove topsoil and subsoil C, respectively

Direction of stand-environment interactive effects on soil C depended on soil depth

1.0 Introduction

Soil organic C (SOC) storage in forest ecosystems is crucial for global climate mitigating efforts (Bowditch and others 2020; Mayer and others 2020) because soils contain more than two-thirds of total forest C stocks (Dixon and others 1994; Yude and others 2011). SOC stock is also a key indicator of overall soil quality (Mayer and others 2020; Wiesmeier and others 2019). The balance between litter input and decomposition determines SOC stocks in forests (Liu and others 2018). This suggests that scientific investigations into stand parameters that govern the quality and quantity of organic matter input and the prevailing environmental factors that control decomposition and stabilization of organic matter are worthwhile to improve our understanding of SOC storage in forests (Adhikari and others 2020; Mayer and others 2020; Rasmussen and others 2018).

In that context, a key stand level parameter for influencing SOC storage in forests is functional identity (Chen and others 2022; Dawud and others 2017). According to the mass ratio hypothesis, functional traits of dominant species determine ecosystem functioning (Grime 1998). In line with this, tree species are commonly grouped into broadleaved and conifer functional groups to examine their effects on SOC storage (Augusto and others 2015; Dawud and others 2017; Prescott and Vesterdal, 2021). Functional traits that are characteristic of most broadleaved species are high litter quality (high nutrient content, low contents of high molecular compounds such as lignin, tannin, etc), high production of fine roots, and more associated microbial communities than most coniferous counterparts (Mayer and others 2020; Vesterdal and others 2013). These traits promote fast litter transformation and incorporation into upper mineral soil layers (Prescott and Vesterdal, 2021; Vesterdal and others 2013). Common functional traits of most coniferous forests are low quality (nutrient-poor litter with

high molecular compounds) and acidic needles, which limit their microbial transformation leading to accumulation of SOC in the forest floor more than broadleaved forests (Dawud and others 2017; Vesterdal and others 2013). Several studies have demonstrated that broadleaved versus conifers functional traits govern topsoil C storage but have little to no impact on subsoil C storage (Dawud and others 2016; Dawud and others 2017; Vesterdal and others 2013). It is worthy of note, however, that allocation of trees species into broadleaved and conifer functional groups in this context may be an oversimplification in some cases because some broadleaved species have functional traits similar to conifers, and vice-versa (Augusto and others 2015; Cools and others 2014).

Mixing tree species belonging to different functional groups (i.e. functional group diversity) increases the portfolio of functional traits in the forest, which promotes delivery of more ecosystem goods, services, and functions than monocultures (Ratcliffe and others 2017; Van Der Plas and others 2016). As a result, more functionally diverse forests are expected to have higher soil C stocks than less diverse forests due to greater productivity and associated litter inputs (Chen and others 2022; Mayer and others 2020). This has intensified calls for multiple species forest management (Sanaei and others 2021; Van Der Plas and others 2016) including planted forests (Messier and others 2021). The response of SOC storage to tree diversity is, however, not consistent due to strong dependence on the environmental context (Chen and others 2022; Fanin and others 2021; Ratcliffe and others 2017). But the factors underpinning this context-dependency of tree diversity effects are usually elusive (Dawud and others 2017; Fanin and others 2021). Consequently, it constraints opportunities to scale-up and generalize research outcomes (Fanin and others 2021; Ratcliffe and others 2017).

According to Wiesmeier et al. (2019), the environmental drivers of SOC storage are broadly categorized into climatic, topographic, and edaphic factors. Climatic factors, namely temperature and precipitation, influence SOC storage via their effects on net primary productivity (NPP) of forest ecosystems that in turn determines above- and below-ground litter input, and also through litter decomposition (Wiesmeier and others 2019). Although the relative importance of temperature and precipitation for SOC storage depends on the limiting factors of soil organic matter (SOM) production and turnover at a given site (Hobley and others 2015), they operate simultaneously and their individual effects are mostly indistinguishable. Consequently, some studies use integrative variables in the form of aridity indices to characterize their combined effects (Adhikari and others 2020; Rasmussen and others 2018). Site topography controls precipitation, water flow paths, water accumulation and discharge that determine site moisture regime and consequently SOC storage (Hobley and others 2015). However, their effects on SOC storage are minor at large scales and often conflate with climatic factors (Adhikari and others 2020; Hobley and others 2015). Among soil factors controlling SOC storage, texture is considered very important due to the interaction of organic matter with soil mineral surfaces and its role in soil water holding capacity (Basile-Doelsch and others 2020; Dynarski and others 2020), which also has consequence for nutrient availability to trees. This reflects in the positive relationship between SOC and silt and/or clay particles in many soils (Ashida and others 2021; Dynarski and others 2020). However, clay content was not a significant driver of SOC in a continental-scale study but rather oxalate-extractable Al, pH, and climate (Rasmussen and others 2018). Oxides and hydro-oxides of aluminum (Al) and iron (Fe) are indicators of soil surface properties particularly related to sorption capacity in the mineral phase (Ashida and others 2021; Rasmussen and others 2018). Al- and Fe-oxides have greater affinity for SOM and higher specific surface area than other mineral surfaces so they correlate positively with SOC stocks

and stability at many sites (Ashida and others 2021; Rasmussen and others 2018). According to Adhikari and others (2020) and also Wiesmeier and others (2019), the importance and strength of environmental factors for SOC storage depends on the soil depth under consideration. Along that line, Hobley and others (2015) found that the importance of climate for SOC storage decreases with soil depth while edaphic factors become more important, but this has rarely been tested in forest contexts in Europe. It is also not clear how the impact of environmental factors on SOC storage discussed above compares with stand composition at different soil layers.

Aside the main impact of environmental factors on SOC storage described above, they also modify the direction and magnitude of functional diversity effects on SOC storage (Fanin and others 2021; Ratcliffe and others 2017). This is in accordance with the general framework that diversity – forest productivity relationships change along environmental gradients (Ammer 2019; Forrester and Bauhus 2016). Such diversity effects on forest productivity along environmental gradients have implications on SOC storage via addition of above- and belowground litter and exudates to the soil (Mayer and others 2020). They also regulate C supply to soil microbes, which contribute substantial necromass and bio-transformed products to SOC pools (Kallenbach and others 2016; Prescott and Vesterdal 2021). According to the stress-gradient hypothesis (SGH; Bertness and Callaway 1994), positive diversity effect is more likely under harsh than under benign environmental conditions. In line with this, Lu and others (2018) found overyielding of Scots pine-oak mixed forests under harsh site conditions more than under benign conditions. On the contrary, Steckel and others (2019) found overyielding of Scots pine-oak mixtures with increase in climatic water supply. This emphasizes that positive diversity–productivity relationships are possible under both harsh and favourable site conditions. Therefore, we might expect functional diversity to increase

forest litter input to the soil under varied site conditions, but that the resulting net effect on SOC stocks would be contingent on the prevailing environmental factors through their impacts on organic matter retention. If this argument holds, then functional diversity should improve SOC storage when those SOC drivers are such that they favor SOM retention over decomposition. For example, Fanin and others (2021) and Ratcliffe and others (2017) found positive tree diversity effects on SOC stocks with increase in water availability. However, is not clear whether this trend is consistent along gradients of climatic and key edaphic factors involved in forest SOC storage in Europe.

The objective of this study is to compare the relative importance of stand (functional identity and diversity) and environmental factors (climate, soil texture, oxalate-extractable Al and Fe) for SOC storage in top (forest floor + 0-10 cm) and subsoil layers (10-40 cm), and to unravel the environmental drivers of context-dependency of functional diversity effects on SOC storage. The forests were in triplets (two-species mixed stands and their corresponding monocultures at the same site) composed of broadleaved-broadleaved (beech-oak) and coniferous-broadleaved (pine-beech; pine-oak) tree species, which were distributed along large gradient of environmental conditions across seven European countries. We characterized functional identity as the basal area (BA) proportion of broadleaved species (beech, oak) while functional diversity was computed as the product of the BA proportions of broadleaved and conifer (pine) species. The SOC stocks were estimated on soil samples from the forest floor (FF) down to 40 cm in 10 cm intervals following procedures described in Osei and others (2021). We tested the hypotheses that:

(H1) forest stand variables (functional identity and diversity) influence topsoil C storage more than environmental factors;

(H2) environmental factors influence subsoil C storage more than stand factors;

(H3) functionally diverse forests improve SOC storage under increased climatic water availability, and higher clay + silt and oxalate-extractable Al contents.

2.0 Materials and Methods

2.1 Study design and site characteristics

This study was conducted in 21 forest triplets across Europe (Fig. 1). A triplet consisted of two-species mixed stand and their corresponding monocultures at the same site. The three forest stands in each triplet were of similar ages (based on tree cores and forest archives) and had homogenous soil conditions based on texture analyses on soil samples in the 10-20 cm depth. The triplets were of three types: beech-oak (*Fagus sylvatica* L. - *Quercus petraea* (Matt.) Liebl.), pine-beech (*Pinus sylvestris* L. - *Fagus sylvatica* L.), and pine-oak (*Pinus sylvestris* L. - *Quercus robur* L. / *Quercus petraea* (Matt.) Liebl.). These tree species are widely distributed in Europe and are very important for forestry.

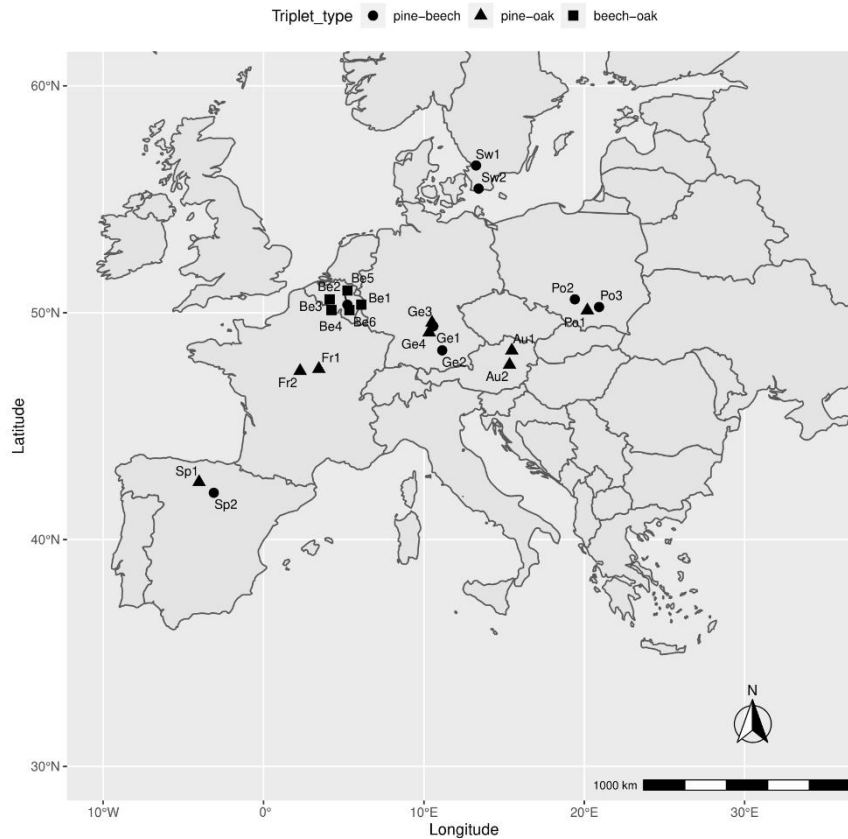


Fig. 1: Map of study sites in seven European countries. Countries were: Au=Austria; Be=Belgium; Fr=France; Ge=Germany; Po=Poland; Sp=Spain; Sw=Sweden.

The triplets were located along wide climatic and edaphic gradients in Europe. Briefly, mean annual temperature ranged from 7.0 to 10.8 °C while mean annual precipitation ranged between 550.0 and 1175.0 mm/year (Table 1). We characterized the combined effect of precipitation (P, mm) and temperature (T, °C) by the de Martonne aridity index (DMI; $P/T+10$; de Martonne 1926). The DMI represent climatic water availability (hereafter “water availability”). The DMI ranged from humid to very humid (30.8 - 60.0 mm/°C; de Martonne 1926). The average clay content across sites was 12.5%, while silt content was 31.5%. The average oxalate-extractable Al and Fe (Al_{ox} and Fe_{ox}) contents, which were used as surrogate for soil surface mineralogy (due to their capacity for mineral-mineral and organo-mineral associations; Wiesmeier and others 2019), were 141.3 mg/kg and 212.0 mg/kg, respectively

(Table 1). The oxalate-extractable metals were highly variable among sites compared to other environmental variables (Table1).

Table 1: Descriptive summary of environmental variables used in this study. The soil variables were determined on composite samples (1 sample per stand in each triplet) from the 10-20 cm soil depth. CV denotes coefficient of variation, calculated as the ratio of standard deviation to the mean.

| Variable | Mean | Range | CV (%) |
|--|-------------|---------------|---------------|
| Mean annual precipitation (P, mm) | 794.7 | 550.0- 1175.0 | 22.1 |
| Mean annual temperature (T, °C) | 8.8 | 7.0 – 10.8 | 12.3 |
| de Martonne index (DMI; P/T+10, mm/°C) | 42.2 | 30.8 - 60.0 | 21.4 |
| Oxalate-extractable aluminium (Al _{ox} , mg/kg) | 141.3 | 62.3 - 534.1 | 88.1 |
| Oxalate-extractable iron (Fe _{ox} , mg/kg) | 212.0 | 39.7-630.6 | 87.9 |
| Clay+silt content (%) | 44.0 | 2.5 – 85.4 | 57.7 |
| Sand content (%) | 56.0 | 16.6 – 93.2 | 45.3 |

2.2 Computation of stand basal areas and functional group proportions

With a diameter threshold of >7 cm, we conducted stem diameter (dbh) inventory in every forest stand. We calculated stand basal areas (BA, m²/ha) from tree dbh values and plot sizes (ha). In each stand, we combined the BAs of the two main species of interest in our study design as stand BA. Subsequently, we partitioned the BA of species in a given stand into broadleaved and conifer functional groups. The broadleaf functional group consisted of BA proportion of beech and/or oak, and the conifer functional group was BA proportion of pine. We grouped beech and oak together because they are both broadleaved species and they had similar effect on SOC storage in a previous study from this dataset (Osei and others 2022).

2.3 Soil sampling and estimation of soil parameters

We placed ten (10) sampling points in each mixed stand and five (5) points each in the corresponding monocultures. At each sampling point, we sampled the forest floor (organic layer above the mineral soil) with 30 cm x 30 cm metal frame. Subsequently, we dug sampling pits in 10 cm interval until 40 cm depth. We estimated total volume (soil + voids + stones) of soil samples in each 10 cm pit by the volume replacement method (Al-Shammary and others 2018) with glass beads. Samples were air-dried, crushed, then passed through 2 mm sieve to separate fine soil (<2 mm), coarse roots (>2 mm), and stones. We picked visible roots in fine soil to reduce their influence on C contents. We separately weighed all the fine soil and the stone fractions. We determined stone volume by water displacement method. Sub-samples of fine soils were ground into powder with Vibratory Disc Mill (Retsch RS 200, Germany) for C and N analyses on all samples (totaling 2080) using CN Analyzer (FlashEA® 1112, USA). Computation of SOC stocks have been described in Osei and others (2021). Soil pH, particle size distribution, and oxalate-extractable metals (Al_{ox} , Fe_{ox}) were determined on samples from the 10-20 cm depth. We determined soil pH in deionized water at a ratio of 1:10 using inoLab pH Level 1 (WTW GmbH, Germany). Particle size distribution was determined by sedimentation method following protocol NF X31-107. The oxalate-extractable metals (Al_{ox} , Fe_{ox}) were extracted by 0.2M ammonium-oxalate at pH 3 according to Blackmore and others (1981), and the concentrations of Al and Fe were determined by ICP.

2.4 Statistical analyses.

In line with our hypotheses, we conducted statistical analyses to compare the effects of stand and environmental factors on SOC stocks (H1 and H2). We also investigated the interactive effects of functional diversity and environmental factors on SOC stocks (H3). We performed

all analyses in R, and tested significance at 95% confidence level in all cases. First, we used the BA proportion of broadleaved functional group (i.e. % BA of beech and/or oak) as a surrogate for functional group identity (hereafter, “functional identity”) in all stands. Following Kirwan and others (2009), we computed the product of BA proportions of broadleaved and conifer functional group (i.e. % BA of pine) to characterize functional group diversity (hereafter, “functional diversity”) in all stands. The coefficient associated with this product tested the effects of the interaction between different tree functional groups (i.e. main effect of functional diversity) on SOC storage. This functional diversity measure was maximum in stands with equal BA proportions of broadleaved and conifer species (i.e. $0.5 \times 0.5 = 0.25$) but zero in complete monocultures of either broadleaved or pine.

Environmental factors considered for testing hypotheses in this study were climatic water availability, soil texture, and soil surface reactivity (oxalate-extractable metals; Fe_{ox} , Al_{ox}) based on their key roles in SOC storage (Adhikari and others 2020; Rasmussen and others 2018; Wiesmeier and others 2019). We excluded soil pH because it can be affected by both overstorey vegetation and environmental factors. However, it will be used as a background information for the interpretation of stand and environmental effects. Predictably, preliminary analyses on the observed values of environmental factors showed high correlations (using Pearson $r > 0.7$ as threshold) among soil metals (Fe_{ox} , Al_{ox} ; $r=0.9$) and among texture variables (clay, silt: $r = 0.85$; clay, sand: $r = -0.92$). Because soil fertility, water holding capacity, and C storage are driven by the fine mineral fractions, we selected both clay content and clay + silt content for subsequent analyses as done by Rasmussen and others (2018). Due to the correlations found above, we needed to select one representative variable for soil metals and one for soil texture. We therefore fitted and compared four full mixed effects models with stone content, basal area, functional identity, functional diversity, and climate (i.e. DMI)

retained in all models but with variable combinations of soil texture and soil metals (i.e. Al_{ox}, clay; Al_{ox}, clay + silt; Fe_{ox}, clay; Fe_{ox}, clay + silt). Mixed effects modeling was appropriate for the hierarchical nature of the study design to address spatial correlation among the three stands of a triplet. It also controlled for other environmental factors not included in our analyses (Zuur and others 2009). Based on the Akaike information criterion (AIC), the model with Al_{ox} and clay + silt content had the lowest AIC. The selection of Al_{ox} model over Fe_{ox} is also supported by the fact that Al oxides have dominance over Fe oxides in the fine mineral phase (Wiesmeier and others 2019). Therefore, the three environmental variables included in the final model were DMI, clay + silt content, and Al_{ox}. The final mixed effect model for testing our hypotheses was as follows:

$$\text{SOC} \sim \alpha 1 + \alpha 2 \text{ stone content} + \alpha 3 \text{ BA} + \alpha 4 \text{ functional identity} + \alpha 5 \text{ functional diversity (FD)} + \alpha 6 \text{ DMI} + \alpha 7 \text{ ClaySilt content} + \alpha 8 \text{ Al}_{\text{ox}} + \alpha 9 \text{ FD*DMI} + \alpha 10 \text{ FD*ClaySilt content} + \alpha 11 \text{ FD*Al}_{\text{ox}} + e_{(\text{triplet})} + \varepsilon \quad (1)$$

$\alpha 1$ is the regression coefficient of the intercept, $\alpha 2$ - $\alpha 11$ are the regression coefficients of the fixed effects, $e_{(\text{triplet})}$ is a random parameter associated with site and ε is the error term. SOC is the soil organic C stock either in the topsoil (FF+0-10 cm), subsoil (10-40 cm), or the total soil layer (FF+0-40 cm). Stone content was included to account for differing stoniness among stands; BA is the total basal area of the main species to account for stand density; functional identity is the BA proportion of broadleaved species (beech and/or oak) in each stand; and functional diversity is the product of broadleaved and conifer (pine) BA proportions. Al_{ox} is oxalate-extractable aluminium (mg/kg); DMI is the de Martonne aridity index calculated from mean annual precipitation and temperature (mm/°C), high values denote increase in climatic water supply. ClaySilt is the sum of clay and silt content (%).

We standardized (mean=0, SD=1) the explanatory variables in all models to allow independent interpretation of interactions and main effects. We represented significant interactions between functional diversity and environmental factors in the mixed models at the mean (0), mean + SD (1), and mean – SD (-1) in graphical moderation analyses. These levels showed the direction of functional diversity effects on SOC storage at average (0), above average (1), and below average (-1) conditions of the interacting environmental factors. Subsequently, we performed variance partitioning to obtain the percentage of variability in SOC explained by fixed effects, random effects, and residuals.

We used *lme4* R package (Bates and others 2015) for mixed effect modeling with restricted maximum likelihood (REML). We conducted model inspections for normality, collinearity (using variance inflation factors, VIF), and heteroscedasticity with *performance* (Lüdtke and others 2021) and *ggResidpanel* (Goode and Rey 2022) R packages. The VIFs of parameters in the models were all less than 3.0, which indicated that multicollinearity did not affect our models. We estimated significance of predictors with Satterthwaite's degrees of freedom method in *lmerTest* R package (Kuznetsova and others 2017). We used *partR2* R package (Stoffel and others 2020) for variance partitioning, and performed moderation analyses with *ggeffects* R package (Lüdtke 2018).

3.0 Results

3.1 Main effects of stand and environmental factors on SOC storage

We have reported the environmental factors used in this study in Table 1. Functional identity was a significant driver of SOC storage in the topsoil (Table 2) and explained about 12.0% of variation in SOC stocks (Fig. 2). Functional diversity was nearly significant ($p=0.05$), and interacted significantly with DMI and sand content. With *ca* 1%, its contribution to total variability in SOC was much lower than that of functional identity (12.0%). In the topsoil, increasing the proportion of broadleaved species in the forest was associated with a reduction in SOC storage (Table 2).

Table 2: Results of mixed effect models (Eq. 1) showing the effect of functional identity (% BA of beech and/oak; broadleaved species), functional diversity (product of broadleaved and pine BA proportions; FD), de Martonne index (DMI; calculated from mean annual precipitation and temperature), clay + silt content, oxalate-extractable aluminium (Al_{ox}), and interactions of FD with environmental factors on soil organic C stocks (Mg/ha). Positive estimate for FD indicates that pine-broadleaved interactions improve SOC storage, and vice-versa. Stand BA and stone content were included as covariates to address contrasted stand density and stoniness among stands. All predictors were standardized (mean=0, SD=1) to allow interpretation of main and interaction effects. Site was fitted as random effect in all models.

| Parameters | FF+0-10 cm | 10-40 cm | FF+0-40 cm |
|---------------------------|----------------------|----------------------|-----------------------|
| Intercept | 55.97 (3.46), <0.001 | 38.79 (2.36), <0.001 | 95.07 (5.41), <0.001 |
| Stone content | -5.71 (1.42), <0.001 | -4.40 (1.12), <0.001 | -10.16 (2.02), <0.001 |
| Stand basal area | -1.85 (1.51), 0.22 | 0.03 (1.19), 0.98 | -1.34 (2.00), 0.50 |
| Functional identity | -9.23 (1.17), <0.001 | -1.31 (0.92), 0.16 | -10.26 (1.53), <0.001 |
| Functional diversity (FD) | -2.36 (1.23), 0.05 | 2.42 (0.97), 0.01 | 0.42 (1.61), 0.79 |
| DMI | 6.06 (4.47), 0.19 | 10.68 (3.12), 0.002 | 17.36 (6.71), 0.01 |
| Clay + silt (ClaySilt) | 2.54 (3.55), 0.48 | 0.05 (2.63), 0.98 | 2.33 (5.00), 0.64 |
| Al_{ox} | -3.15 (3.12), 0.32 | 1.19 (2.20), 0.59 | -3.51 (4.64), 0.45 |
| FD x DMI | -5.74 (1.70), 0.001 | 6.00 (1.36), <0.001 | 0.74 (2.24), 0.74 |

| | | | |
|-----------------------|--------------------------|--------------------------------|----------------------------|
| FD x ClaySilt | 2.90 (1.43), 0.04 | -0.88 (1.14), 0.44 | 2.47 (1.87), 0.19 |
| FD x Al _{ox} | 1.17 (1.07), 0.27 | -5.18 (0.85), <0.001 | -4.68 (1.40), 0.001 |

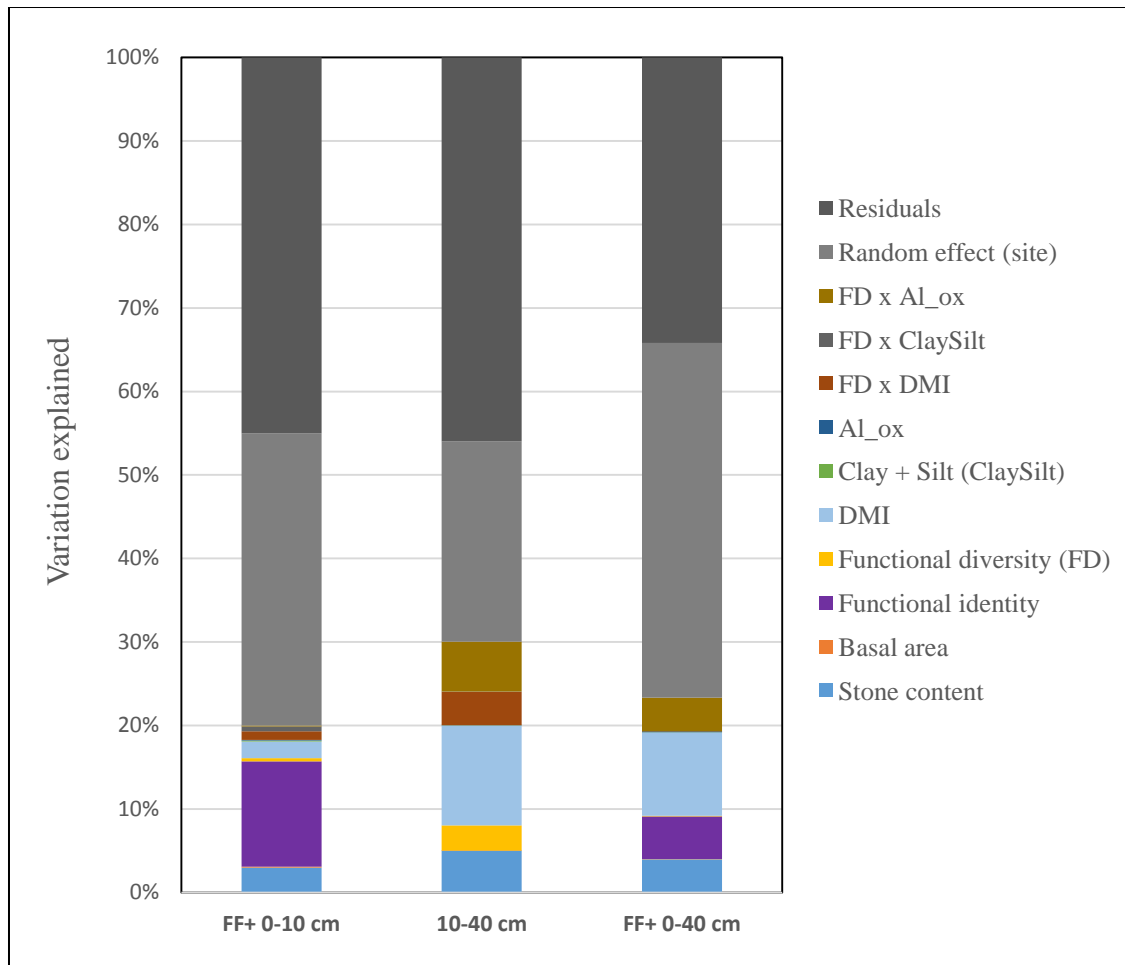


Fig. 2: Percentage of variation in SOC stocks explained by functional identity (% BA of beech and/or oak; broadleaved species), functional diversity (product of broadleaved species and pine BA proportions; FD), de Martonne index (DMI; calculated from mean annual precipitation and temperature), clay + silt content, oxalate-extractable aluminium (Al_{ox}), and interactions of FD with environmental factors as predictors of soil organic C stocks (Mg/ha) in mixed effect models (Eq. 1 at section 2.4). Stand BA and stone content were included as covariates to address contrasted stand density and stoniness among stands. All predictors were standardized (mean=0, SD=1) to allow computation of variance explained by main and interaction effects independently. Site was fitted as random effect in all models.

None of the three environmental factors had significant main impact on SOC storage in the topsoil (Table 2). The main effects of environmental factors (DMI, Clay + silt, Al_{ox}) together were responsible for only 2.2% variability in SOC stocks in the topsoil (Fig. 2). In the subsoils, functional diversity was significantly related to SOC storage but not functional identity. Amongst the environmental factors, DMI significantly improved SOC storage in subsoils and explained 12.0% variation while the other environmental factors were not significant (Table 2; Fig. 2). The percentage of variability in subsoil C storage explained by stand factors (3.0%) was just a quarter of variability explained by the environmental factors (12.0%; Fig. 2). Considering the total soil layer (FF+0-40 cm), functional identity but not functional diversity, had significant control on SOC stocks. Among the environmental factors, only climatic water availability had significant (and positive) main effects on SOC storage in the total soil depth.

3.2 Interactions between functional diversity and environmental factors

The effect of functional diversity on SOC storage in the topsoil (FF+10 cm) was dependent on climatic water availability and soil texture (Table 2). In the subsoils, climatic water availability also moderated the effect of functional diversity on SOC storage, as well as Al_{ox} (Table 2). Under increasing climatic water availability, functional diversity effects on SOC storage shifted from negative in the topsoil to positive in the subsoil (Fig. 3).

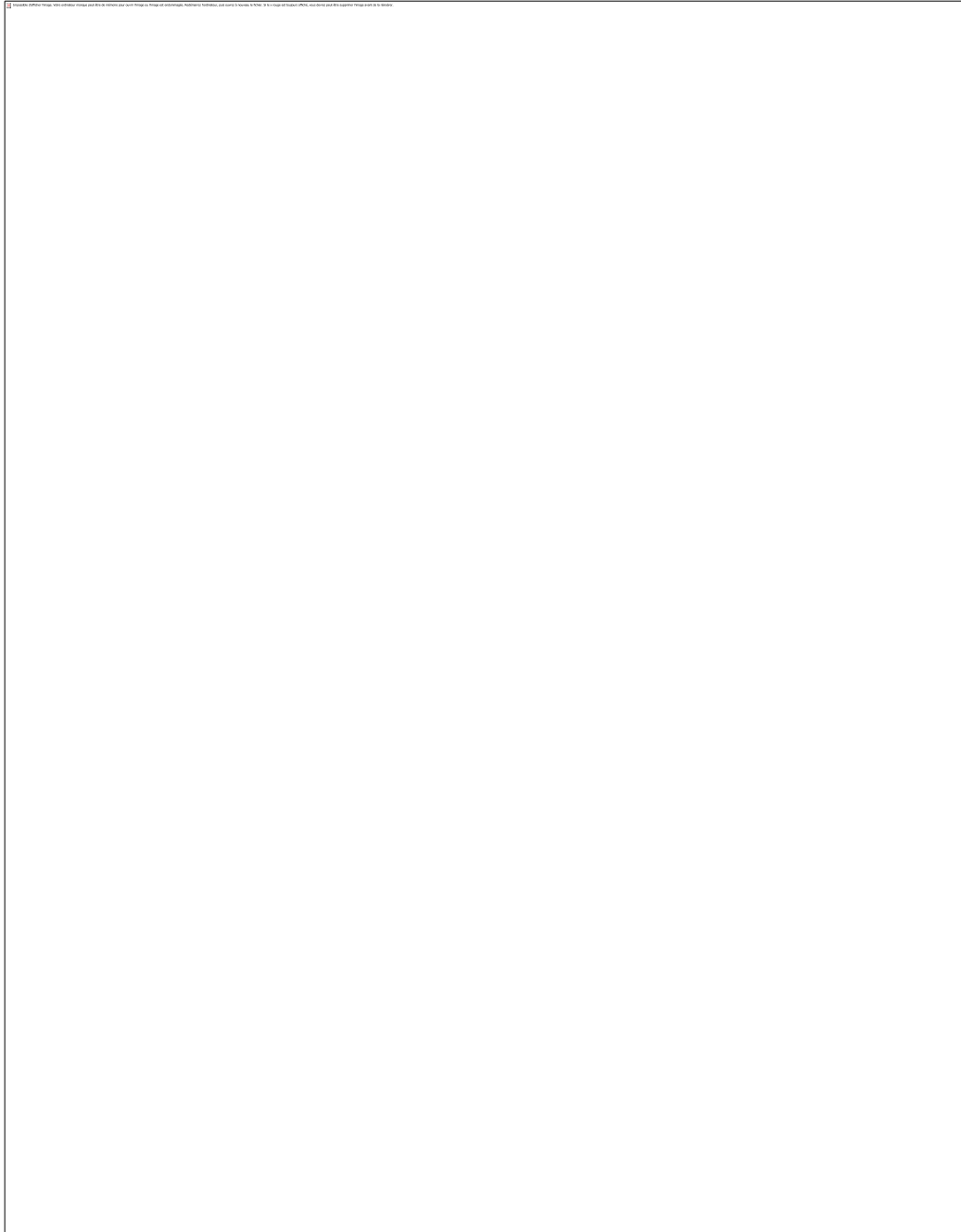


Fig.3: Significant interactive effects of functional diversity and environmental factors on soil organic C (SOC; Mg/ha) in the topsoil (A: de Martonne index – DMI, B: clay + silt content – ClaySilt) and in the subsoil (C: de Martonne Index – DMI, D: Oxalate-extractable aluminium – Al_{ox}). The figure shows the direction of functional diversity effects on SOC at below average (mean-SD = -1), average (0), and above average (mean + SD = 1) values of the environmental factors, when all other covariates are held constant at their mean values in mixed effect models (Eq. 1 at section 2.4). See Table 2 for full statistical results.

In the topsoil, increase in functional diversity had slightly negative effect on SOC storage at below average clay + silt content (Fig. 3B). The Al_{ox} content changed the direction of functional diversity effects on subsoil C storage from positive at below average levels to negative with increasing Al_{ox} . The variance partitioning demonstrated that the interaction of functional diversity with the three environmental factors explained about 10% of variability in subsoil C storage. This explained variance was 5.9 times the variance they (the interactions) explained in topsoil C stocks (1.7%; Fig. 2).

4.4 Discussion

4.1 Functional identity is the main driver of topsoil C storage

The broadleaved species (beech, oak) were combined as a functional group because they had similar effects on SOC at all soil depths (Osei and others 2022). We computed functional diversity as the product of basal area proportions of broadleaved species (beech, oak) and the conifer (pine). Because this study involved three different triplet types (pine-beech, pine-oak, beech-oak), we combined the entire datasets and analyzed them as a unit in order to utilize the whole gradients in environmental conditions covered by this study. Our findings that forest stand factors, particularly functional identity, have stronger control on topsoil (forest floor + 0-10 cm depth) C storage than environmental factors agrees with the first hypothesis (H1). This lend support to previous findings that different regulatory mechanisms control C accumulation in top versus subsoil layers (Chen and others 2022; Mayer and others 2020). This finding implies that the functional group of tree species in a forest is more important for forest floor and upper mineral soil C accrual than the environmental factors in this study. Dawud and others (2017) indicate that strong functional group effects on topsoil C storage

reflect litter chemistry, associated soil biota, and root dynamics. Broadleaved forests like beech and oak usually have relatively higher foliar and root litter quality (indicated by high N and P concentrations, low lignin/N ratios, etc) than most coniferous forests (Chen and others 2022; Krishna and Mohan 2017). Similarly, broadleaved litter often has higher pH values than pine, which reduces soil acidity and spur microbial transformation (Krishna and Mohan 2017; Mayer and others 2020). Likewise, tree functional groups have distinctive signatures on the identity, abundance, and diversity of soil biota (Prescott and Vesterdal 2021). On average, broadleaved species often support more soil biota than most coniferous species (Prescott and Vesterdal 2021; Vesterdal and others 2013). According to Prescott and Vesterdal (2021), broadleaved species like beech and oak promote earthworms, bacteria, and mull forest floor forms. These species have decomposition pathways dominated by microbial transformations, macrofaunal detritivorous transformation, and bioturbation by earthworms (Prescott and Vesterdal 2021). The acidic nature of the soils in this study (pH 3.8 - 4.7) may, however, limit these biotic processes. The afore-mentioned traits of broadleaved species that support faster litter decomposition explain the negative main effects of functional identity (in terms of beech and/or oak proportion) on topsoil C storage (Table 2). In Bavaria, Germany, replacement of spruce and Scots pine by beech led to a 38% to 45% decrease in forest floor C stocks but no changes occurred in the mineral soil (Prietzl and Bachmann 2012). Similarly, Matos and others (2010) found that admixture of oak (*Quercus petraea*) in pure stands of Scots pine led to a reduction in SOC stocks in the topsoil. Counter-intuitively, this quick transformation of broadleaved litter in the topsoil by decomposers is a strategic pathway for stabilization of organic matter in the soil (Prescott and Vesterdal 2021). This is because soil microbes transform organic matter into novel compounds that have high residence time and are preferentially sorbed onto soil mineral surfaces (Kallenbach and others 2016; Prescott and Vesterdal 2021). On the other hand, pine forests have recalcitrant and acidic litter less

favorable for microbial transformation, and that results in C accumulation in topsoil layers (Dawud and others 2017; Krishna and Mohan 2017; Mayer and others 2020). The strong effect of functional identity (in terms of beech and/or oak proportion) on topsoil C in this study implies that the dominant tree functional group in a forest controls topsoil C storage per the ‘mass ratio hypothesis’ (Grime 1998). However, our findings should not be generalized for all broadleaved and conifers species as their effect on SOC storage could be different from those species studied herein (Augusto and others 2015; Cools and others 2014)

4.2 Climatic water availability is the main driver of subsoil C storage

In contrast to the topsoil layers, environmental factors (principally climatic water availability) had major control on subsoil C storage as expected (H2). This represents a shift from a species composition-driven C storage in the topsoil to an abiotic-driven C storage in the subsoil. This finding is not so surprising given that the footprint of tree species on SOC storage is in general much lower or even absent in deeper soil layers (Dawud and others 2017; Gray and others 2016) while abiotic factors become more important (Gray and others 2016; Hobbey and others 2015). The stronger impact of climatic water availability on subsoil C storage than the topsoil contradicts findings by Gray and others (2016) and Hobbey and others (2015) that climatic influence on SOC storage decreases with depth. Emerging understanding that fine roots and their associated microorganisms are the major sources of stable SOC in forest ecosystems (Dynarski and others 2020; Gross and Harrison 2019; Hobbey and others 2015; Prescott and Vesterdal 2021) implies that abiotic factors that impact root productivity and soil biota are crucial for SOC storage. In this respect, the positive effect of climatic water availability on subsoil C stocks could be explained by the positive impact of climatic water

availability on fine root productivity and microbial community dynamics as well as their subsequent transformations into SOM. This has been confirmed in global syntheses in which climate was the main abiotic driver of fine root traits (Freschet and others 2017) and microbial abundance in soils (Serna-Chavez and others 2013).

Surprisingly, soil texture (i.e. clay + silt content) was not a significant main driver of SOC in this study, which confirms findings of Rasmussen and others (2018) that other abiotic parameters such as climate are better predictors of SOC storage and stabilization than texture at large spatial scales. This is because similar sized clay and silt particles usually have different mineral constituents (phyllosilicates, oxyhydroxides and aluminosilicates, organo-metal complexes), which differ in their surface area, reactivity, solubility, and sorptive capacity (Rasmussen and others 2018; Wiesmeier and others 2019). Therefore, clay + silt content can mask the diversity of constituent mineral properties in different clay types and may not effectively capture the specific SOC storage or stabilization mechanisms in the forests we studied (Rasmussen and others 2018). Additionally, in acidic forest soils like those in this study ($\text{pH-H}_2\text{O} = 3.8 - 4.7$ in 10-20 cm depth), the mineral composition of the clay fraction is expected to have more impact on SOC sorption than soil particle sizes (e.g. clay or clay + silt content), in contrast to near neutral agricultural soils. Similarly, Al_{ox} did not have main effects on SOC storage although its positive effect on SOC storage has been reported in several studies (Poehlau and others 2021; Rasmussen and others 2018). It has also been cited as a principal driver of SOC storage and stabilization in acidic forest soils like those in this study (Eusterhues and others 2005). The likely explanation for its non-significant effect in this study could be that Al_{ox} is more associated with the highly processed SOC fraction as organo-mineral and organo-metallic complexes (Eusterhues and others 2005) than the total SOC stocks that is composed of organic matter fractions at varying degrees of decomposition.

Another plausible explanation could be that humid conditions intensify weathering of parent material that favour the formation of Al-SOM complexes (Doetterl and others 2015; Rasmussen and others 2018) so the strong effects of climatic water availability observed in this study probably masks Al_{ox} effects.

4.3 Functional diversity effects on SOC storage change along environmental gradients

Expectation of positive effect of functional diversity on SOC stocks with increase in climatic water availability, clay + silt content, and oxalate-extractable Al was only partially supported. Climatic water availability interacted with functional diversity in both top- and subsoil, but in each soil layer, functional diversity also interacted with another environmental driver, and the latter interactions explained a larger part of the total variability in SOC in subsoil and the total soil layers. This confirms findings by Ratcliffe and others (2017) that water availability is the major driver of context-dependency of tree diversity-ecosystem functioning relationships. The key finding of this study is that higher functional diversity had negative effects on topsoil C storage with increase in climatic water supply but shifted to positive in the subsoil. This is in agreement with Chen and others (2022) who found negative effect of functional diversity on SOC in the organic layer under high climatic moisture index. Positive effects of functional diversity on topsoil C storage with decreasing water availability contradicts our hypothesis (H3) but the reverse situation in the subsoil is in agreement with expectations. According to Chen and others (2022), positive effect of functional diversity on tree productivity and associated litter inputs could be counteracted by priming at drier sites, leading to low SOC stocks under diverse forests on drier sites. Mixing broadleaved species with conifers (like pine) would usually improve forest productivity (Brassard and others 2013; Ma and others 2019; Steckel and others 2019) and lead to the production of “surplus carbon” (*sensu* Prescott

and others 2020). The “surplus C” is produced when leaf cells produce more photo-assimilates than they are able to use for primary metabolism because tree growth is more constrained by the availability of nutrients, water, or temperature than photosynthetic C fixation (Jactel and others 2018; Prescott and others 2020; Steckel and others 2019). Because retention of surplus carbohydrates can damage leaf cells, much of the surplus C are transported through the phloem to active sinks such as roots (Prescott and others 2020). The distribution of this “surplus C” in the roots with soil depth would then change as a function of climatic water availability (DMI). High water availability would enhance forest productivity and intensify competition for soil resources (Steckel and others 2019) that shift fine root production down to deeper soil layers (Brassard and others 2013; Ma and others 2019). This would result in root complementarity (broadleaved vs conifer) and a more efficient exploitation of the soil volume in mixed stands than monocultures (Bolte and Villanueva 2006; Finér and others 2017), with attendant addition of fine root litter to the soil matrix (Dawud and others 2016; Leuschner and others 2001; Ma and Chen 2016). Such root productivity also enhances supply of root exudates to soil microbial communities, which are major components of subsoil C pools (Dynarski and others 2020; Kallenbach and others 2016; Prescott and Vesterdal 2021). Such possible shift of fine root production in functionally diverse forests to subsoils with increases in climatic water availability could explain the opposite effects observed for SOC storage in the topsoil (Fig. 3). Alternatively, the negative effects of functional diversity on topsoil C stocks under increasing climatic water availability (Fig. 3) could be due to accelerated litter decomposition driven by the joint effects of litter diversity (Hattenschwiler and Gasser 2005) and wet conditions (Fanin and others 2021; Wiesmeier and others 2019).

Soil texture influenced functional diversity-SOC stock relationship in the topsoil but not in the subsoil. This agrees with Ratcliffe and others (2017) who found soil texture as a driver of context dependency of species richness effects on topsoil C cycling in European forests. In agreement with the third hypothesis (H3), higher functional diversity had negative effect on C stocks in the topsoil with decreasing clay + silt content (i.e. increasing sand content). We posit that soils with low clay and silt content usually have low sorptive capacity (Poeplau and others 2021; Wiesmeier and others 2019) to bind root litter inputs resulting from the surplus root C. On the other hand, functional diversity improved subsoil C storage under decreasing Al_{ox} content, in contrast with our expectations. (H3). This outcome could be due to enhanced fine root productivity, exploration, and litter inputs in the subsoil matrix in response to high phosphorous (P) availability under low Al_{ox} contents (Ma and Chen 2016; Pena and Torrent 1990) because P is the most limiting soil nutrient in most forests (Pena and Torrent 1990). This is premised on the fact that oxides of Al and Fe are the primary adsorbents of P (Pena and Torrent 1990; Sibanda and Young 1986) so P becomes available for plant uptake in soils with low Al_{ox} and Fe_{ox} contents (Pena and Torrent 1990), yet not in all cases (Sibanda and Young 1986).

4.5 Conclusion

This study assessed the relative impact of stand composition factors (functional identity, functional diversity) and environmental factors (climatic water availability, clay + silt content, Al_{ox}) on SOC storage in topsoil (FF+0-10 cm) and subsoil layers (10-40 cm) for triplets of monospecific and two-species forest stands spanning a large gradient of environmental conditions in Europe. It also investigated the environmental drivers of context-dependency of functional diversity effects on SOC storage. Regarding topsoil C storage, functional identity

(broadleaved – oak/beech vs coniferous – pine) was significant but functional diversity (product of basal area proportions of broadleaved species and pine) was marginally significant; they together explained 13.0% variability in SOC storage. In the same soil depth, none of the environmental factors was significant (in terms of main effects) but climatic water availability and clay + silt content had significant interactions with functional diversity. In the subsoil, functional identity was not significant but functional diversity was significant (explained 3.0% variability) and had significant interactions with climatic water availability and Al_{ox} . Climatic water availability was the only environmental factor that had significant main effect on SOC stocks in the subsoil (accounted for 12.0% variability) and the total soil depth. It also had significant interactions with functional diversity in both top and subsoils, which supports earlier studies that climatic water availability is the most important driver of context-dependency of tree diversity effects on SOC storage. The results indicate that stand factors have stronger impact on C storage in topsoil than the environmental factors while the opposite occurs in the subsoil. Among the stand factors, the dominant functional group in the forest shapes C storage in the topsoil and total soil layers but functional diversity of the forest is more important for improving SOC storage in subsoils. The drivers (and direction) of context-dependency of functional diversity effects on SOC storage were dependent on the soil depth under consideration. The results imply that the direction of functional diversity effects on SOC storage along environmental gradients is difficult to forecast due to the soil depth-dependency involved.

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